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The Biology of *Hoplitis (Robertsonella) simplex* (Cresson), with a Synopsis of the Subgenus *Robertsonella* Titus

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Abstract.—Three species are recognized in *Hoplitis (Robertsonella)*: *H. micheneri* Mitchell, *H. nemophilae* Neff, and *H. simplex* Cresson. *Hoplitis nemophilae* is described and a key is provided for the subgenus. The nesting biology of *H. simplex* is described, along with notes on the biology of the other species. *Hoplitis simplex* is a vernal bee that gathers mud to construct nests in pre-existing cavities. It appears to be an oligolege of the Boraginaceae: Hydrophylloideae and constructs 1–3 cells per day. The last larval instar commences defecation the day after the last larval molt and initiates construction of the operimentum (a secreted lining on the anterior cell partition) well before the completion of feeding.

Robertsonella Titus is a small group of osmiine bees of eastern North America (Tamaulipas, Mexico to Connecticut, USA). Although originally given generic status, it currently is considered to be a subgenus of *Hoplitis* Klug (Hurd and Michener 1955; Michener 2007). While studying the pollination biology of *Nemophila phacelioides* Nutt. (Boraginaceae: Hydrophylloideae) in central Texas, I commonly encountered two *Robertsonella* species at *N. phacelioides* flowers. One species was particularly abundant at the Brackenridge Field Laboratory (BFL) of the University of Texas, in Austin, Texas and was found to regularly nest in small diameter trap nests. Since nothing had been reported on the nests of any *Robertsonella* species, a study was undertaken of its nest biology.

Problems arose when attempting to identify the two species. Mitchell (1962), recognized two species of *Robertsonella* from Texas: *Hoplitis simplex* (Cresson) and *Hoplitis gleasoni* (Titus). He noted that he might have errantly associated the sexes of *H. simplex* when he described what he believed to be the previously unknown male of that species. If true, this would require a new name for his new male. An analysis of the distribution of males of the species of *Robertsonella* was undertaken to resolve this problem. Here I report on the results of that analysis along with data on the biology of *H. simplex*.

MATERIALS AND METHODS

All timings of foraging and nest construction were performed at Brackenridge Field Laboratory (BFL) of the University of Texas at Austin (30.285° N 97.781° W) with either a handheld stopwatch or a digital watch. Activities were timed to the nearest second for nest provisioning and construction and to 0.1 sec for foraging behavior at flowers. Casual observations of *Hoplitis simplex* began in 1982 with timings of provisioning and nest construction occurring during the springs of 1986–1990 and 1994 and 1995. The possibility for observations of *H. simplex* at BFL were greatly curtailed after 1999 when a deer population explosion devastated the forbs at BFL, leading to a precipitous decline of the *H. simplex* population. Detailed observations of larval development and cocoon construction were made using split trap nests in 1987 and 1988. Morphological terminology follows Michener (2007). Distributions

are recorded at the county level. Abbreviations are as in Neff (2004). Statistics were calculated with JMP® and are presented as the mean ± 1 s. d.

Institutions or collections where paratypes are deposited, as well as the sites for other material examined, are as follows: American Museum of Natural History, New York, New York (AMNH); Snow Entomology Museum, University of Kansas, Lawrence, Kansas (KSEM); Museum of Entomology, Florida State University, Tallahassee, Florida (FSCA): Texas A & M University Insect Collection, College Station, Texas (TAMU); U. S. National Museum of Natural History, Smithsonian Institution, Washington, D. C. (USNM); Utah State University Bee Biology and Systematics Laboratory, Logan, Utah (BLCU); North Carolina State University Insect Collection, Raleigh, North Carolina (NCSU); Purdue University Insect Collection, West Lafayette, Indiana (PURC); M. S. Arduser Collection, St. Louis, Missouri (MSAC); Central Texas Melittological Institute, Austin, Texas (CTMI); Brackenridge Field Lab Collection, The University of Texas at Austin, Austin, Texas (BFLC).

TAXONOMIC HISTORY

Robertsonella has had a troubled taxonomic history. The name was originally proposed by Titus (1904) for *Robertsonella gleasoni* Titus, a new genus and species of megachilid bee from Grand Island, Illinois. For many years there was confusion as to identity of these bees since, while the males are fairly distinctive among osmiine megachilids, the females are not. Females of *Alcidamea*, another group previously given generic status but now also considered to be a subgenus of *Hoplitis*, were commonly misidentified as *Robertsonella*, leading to a misleadingly expansive distribution (Graenicher 1909; Hurd et al. 1980; Michener 1941, 1947; Pearson 1933) and some spurious host-parasite associations (Swenk 1914; Hurd 1979) for *Robertsonella*. In the first revision of *Robertsonella*, Michener (1938) found *Heriades simplex* Cresson to be a senior synonym of *R. gleasoni*. He also relegated *Robertsonella crataegina* Cockerell, a species described from Texas (Cockerell 1909), to subspecific status under *R. simplex*. Hurd and Michener (1955) later placed *Robertsonella* as a subgenus of *Hoplitis* stating that its primary distinguishing character, the near horizontal metanotum, did not outweigh its many similarities with *Hoplitis*. Later, the placement of *Robertsonella* in *Hoplitis* was strengthened by the discovery that *Robertsonella* shared the key synapomorphy of *Hoplitis*, the flap-like gradular projections of the male S6 (Griswold and Michener 1998; Michener 2007).

Species concepts in *Robertsonella* were greatly altered by Mitchell (1962). He described a new species, *Hoplitis (Robertsonella) micheneri* Mitchell, from Kansas and Georgia, resurrected *gleasoni* as a distinct species (with *crataegina* as a synonym), and described a new male that he associated with *H. simplex*. Although he separated the females of *gleasoni* and *simplex* in his key on the basis of their tergal punctation (close and coarse in *H. gleasoni*, finer and sparser in *H. simplex*), he stated in the text that the females of the two species could not be reliably separated. He went on to note that he might have erred when he associated his new male with *H. simplex*, a species previously known only as a female. A reexamination of the types of *H. simplex* and *H. gleasoni*, plus an analysis of the distribution of males, discussed below, involving more material than was available to Mitchell, indicates the sexes were indeed misassociated. A new species is described below for the male he incorrectly assigned to *H. simplex*.

A fourth species, *Robertsonella himachalli* Gupta was described from northwestern India in 1991, apparently under the erroneous impression that females of *Robertsonella* have an apico-median clypeal projection. If validly placed, this would be a remarkable range extension. Although I

have seen no specimens of this species, it is clear from the description and the characters used in the generic key (Gupta 1991, 1999) that this large (12 mm), metallic-blue species, the males of which have an apically emarginate T6 does not belong in *Robertsonella* and almost certainly is not a *Hoplitis.*

SYSTEMATICS

Hoplitis (Robertsonella) micheneri Mitchell

Hoplitis (Robertsonella) micheneri Mitchell, 1962. N. C. Agr. Expt. Sta. Tech. Bul. 152: 65 (m, f)

Distribution.—USA: **Florida** (*Jackson, Suwannee*); **Georgia** (*Cobb, Fulton, Hamilton*): **Kansas** (*Douglas, Miami, Riley*); **Missouri** (*Shannon, Stoddard*); **North Carolina** (*Richmond*).

While sometimes locally abundant, (indicated by multiple collections from Suwannee Co., Florida), this bee appears to be rare with a possibly disjunct distribution. Populations are known from Kansas and Missouri and the southeastern U.S. (Florida, Georgia and North Carolina) (Fig. 1). Originally known only from Kansas and Georgia (Mitchell 1962), newer records from Missouri, North Carolina and Florida suggest additional fieldwork may eliminate the current disjunction in its distribution. Available floral records for females indicate it is specialist on *Amorpha fruticosa* (L.) (Fabaceae), a widespread shrub of the eastern U. S. It has repeatedly been collected on *A. fruticosa* in Kansas and Missouri and pollen analysis of the females from Florida collected at a nest site indicated scopal loads of nearly pure *A. fruticosa* pollen. Other floral records include *Rubus* (Rosaceae) and *Melilotus officinalis* (L.) Pall. (Fabaceae). *Hoplitis micheneri,* like other *Robertsonella,* is a vernal bee with flight records from 16 April (in Florida) to 13 June (in Missouri). Labels from a series of females from Suwannee River State Park, Florida collected by L.

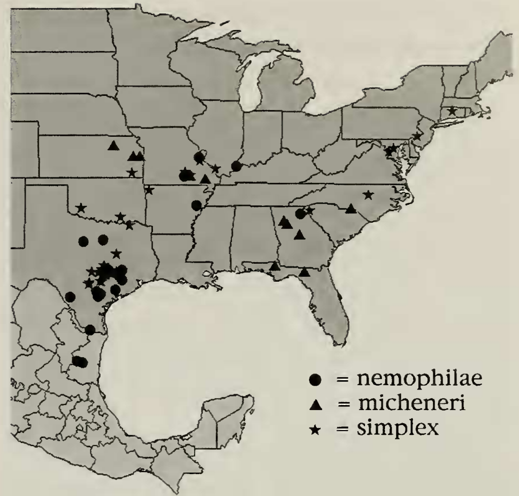

Fig. 1. Map of the distribution of *Hoplitis (Robertsonella)* spp. based on males.

Stange stated they were "around small holes in old trees", suggesting this species utilizes small preexisting holes for its nests.

Females are about the same size as *Hoplitis simplex* (HW = 2.19 ± 0.11 mm, 1.84–2.44, n=33; BL = 7.31 ± 0.52 mm, 6.16–8.48, n = 25) and are easily separated from other *Robertsonella* by having T1 shining with the punctures very fine and sparse. Males have the same pattern of facial pubescence as *H. nemophilae* but are about the same size as *H. simplex* (HW = 1.94 ± 0.05 mm, 1.79–2.20, n = 10 in *H. micheneri* vs. 1.92 ± 0.10 mm, 1.68–2.12, n = 66 in *H. simplex*). Males are distinctive in having S3 deeply emarginate (Fig. 5) [emargination of S3 very shallow and obscure in *H. nemophilae* and *H. simplex* (Fig. 4)].

Hoplitis (Robertsonella) simplex (Cresson)

Heriades simplex Cresson, 1864. Ent. Soc. Phila. Proc. 2, p. 384, f.

Robertsonella gleasoni Titus, 1904. N. Y. Ent. Soc. Jour. 12, p. 23, f, m.

Robertsonella crataegina Cockerell, 1909. Ann. Mag. Nat. Hist. (8) 4. 28.

Robertsonella simplex simplex: Michener, 1938. Ent. News 49, p. 131.

Robertsonella simplex crataegina: Michener, 1938. Ent. News 49, p. 130.

Hoplitis (Robertsonella) gleasoni: Mitchell, 1962. N. C. Agr. Expt. Sta. Tech. Bul. 152: 65 (m, f in part)

Distribution.—USA: **Arkansas** (*Washington*); **Connecticut** (*Hartford*); **Illinois** (*Jackson*); **Kansas** (*LaBette*); **Missouri** (*Dent, Jefferson, Shannon*); **New Jersey** (*Camden*); **North Carolina** (*Wake*); **Oklahoma** (*Atoka, Kiowa*); **South Carolina** (*Anderson*); **Texas** (*Bastrop, Bee, Bexar, Blanco, Burleson, Goliad, Gonzalez, Grimes, Guadalupe, Karnes, Lamar, Lee, Limestone, Travis, Washington, Williamson*); **Virginia** (*Fairfax*).

Males of *Hoplitis gleasoni* and *H. simplex* (*sensu* Mitchell 1962) are easily separated by the characters in the key of Mitchell (1962). Males of *Hoplitis gleasoni* (*sensu* Mitchell 1962) occur from Connecticut and New Jersey to central Texas while males of *H. simplex* (*sensu* Mitchell 1962) are known from Indiana and North Carolina to central Tamaulipas (Fig. 1). As noted by Mitchell (1962), the female type of *H. simplex,* and females from the type series of *H. gleasoni* are not distinguishable so it is not obvious why the new male described by Mitchell was assigned to *H. simplex*. As the female type of *Hoplitis simplex* (Cresson) is from Connecticut but the nearest male of *H. simplex* (*sensu* Mitchell 1962) occurs some 1300 km away while a male of *H. gleasoni* (*sensu* Mitchell 1962 is known from Connecticut (Fig. 1) , it seems clear that the sexes were misassociated in Mitchell (1962). Thus, the original judgment of Michener (1938), that *H. gleasoni* is a junior synonym of *H. simplex,* is correct and *H. simplex* sensu Mitchell needs a new name that is provided below.

Males of *Hoplitis simplex* are easily distinguished from other *Robertsonella,* and all other North American osmiines, by the long mandibular fringe and the short, dense, appressed pubescence obscuring the clypeal surface. Females of *H. simplex* can be distinguished from *H. micheneri* by the characters listed above and in the key. Although females of *H. simplex* are, on average, slightly larger and more coarsely punctate than those of *H. nemophilae,* their size ranges overlap greatly, and, as the coarseness of the punctation varies with size, that character does as well.

Hoplitis simplex appears to be an oligolege of the Boraginaceae: Hydrophylloideae. The vast majority of floral records for females are for various *Nemophila* and *Phacelia* species. The only plants from which I have observed *H. simplex* females collecting pollen are *Nemophila phacelioides* Nutt., *N. sayersensis* Simpson *et al., Phacelia congesta* Hook. and *P. strictiflora* (Engelm. & Gray) Gray in Texas (all Boraginaceae: Hydrophylloideae). Unfortunately, there are very few floral records for specimens from the northern part of its range. *Hoplitis simplex* is a vernal bee, active from mid March and April (in Texas) to late May (in Connecticut). A number of *simplex*-like females have been collected in Maryland in early June, but as no males were associated with these specimens, it is not clear if they are *H. simplex* or *H. nemophilae.*

The nest biology of *H. simplex* is described below.

Hoplitis (Robertsonella) nemophilae Neff, new species

Hoplitis (Robertsonella) simplex: Mitchell, 1962. N. C. Agr. Expt. Sta. Tech. Bul. 152: 66. (m, f in part)

Diagnosis.—Males of *Hoplitis nemophilae* are distinguished from males of *H. simplex* by the longer, more erect clypeal pubescence, shorter mandibular fringe. They differ from *H. micheneri* by the weakly emarginate margin of S3 (strongly emarginate in *H. micheneri*). Females of *H. nemophilae* differ from those of *H. micheneri* by their denser punctation of T1 and lack the antero-median scutellar groove of that species. As noted above, females of *H. nemophilae* tend to be smaller and more finely punctate than those of *H. simplex,* but I know of no characters that consistently

distinguish females of *H. nemophilae* and *H. simplex*.

Description.—**Male**: Measurements: BL = 5.84 ± 0.32 mm, 5.04–6.65, n = 21; HW = 1.70 ± 0.08 mm, 1.54–1.84, n = 57. *Head*: Face approx. 1.2 × as broad as long, eyes convergent below (UIOD 1.4 × LIOD). Clypeus slightly convex, apical margin nearly straight, disc shining with fine, subcontiguous punctures. Supraclypeal area, parocular area, frons, vertex and gena finely, densely punctate. Labrum with apical margin weakly concave; basal width approx. 1.6 × length; apical width subequal to length; basal 1/3 to 1/2 smooth and shiny with very fine, very sparse punctures, punctures of distal half stronger, denser. Lateral ocelli closer to vertex than to eye (OC-O/OC-V = 1.5) with distance between lateral ocelli subequal to distance from lateral ocelli to eye. Scape slender, unmodified (scape length 2.8 times apical width); pedicel completely exposed; length flagellum (excluding pedicel) 5× scape length; flagellar segments (except first which tapers and is about as long as its apical width) slender, simple, about 1.5 × as long as wide. Gena about as wide as eye medially (in lateral view), tapering below. Hypostomal area shining, sparsely punctate. Mandible bidentate. Extended tongue length (glossa + prementum 2.0–2.2 mm, roughly 1.3 × head length). Ratio lengths labial palps: 3:6:1:1. Four maxillary palps, very short, fourth greatly reduced. *Thorax*: Scutum 2.9 × as long as scutellum, TTW = scutal length. Discs of scutum and scutellum shiny, with strong deep punctures approx 1–2 PW apart, scutellum densely punctate on posterior margin. Tegula shining, sparsely punctate. Metanotum dull, roughened, obscurely punctate. Propodeal triangle shining, impunctate, with narrow, shallowly, irregularly quadrately pitted apical area. Propodeal surfaces outside triangle roughened posteriorly, with shallow dense punctation more evident on anterior surfaces. Mesepisterum with strong dense punctures, punctures larger than on scutum. Legs normal. *Abdomen*: Terga shining, punctures fine, 1–3 PW apart, becoming slightly finer, denser towards distal margins. Terga 3–7 with narrow, impunctate distal margins, impunctate areas broadest on T6 and T7 which are slightly upturned, flange-like. T6 with minute lateral tooth, T7 rounded apically and with disc weakly depressed. S2 subconvex, most of apical margin straight, with dense, shallow punctation. Apical margin S3 very weakly emarginate medially, otherwise nearly straight, punctures as in S2 laterally but becoming very fine and dense medially. Margin S4 straight, punctures as in S2. Margin S5 straight but more rounded laterally, punctures as in S4. Margin S6 more convex but almost straight medially, surface smooth, nearly impunctate. S4–6 with narrow, translucent gradular flaps. S7, S8 and genital capsule as in figure 25 of *H. simplex sensu* Mitchell (Mitchell, 1962); gonocoxites with hairs of ventral surface erect, primarily in median portion. *Vestiture*: Hair all pale, sparse, erect except: clypeus with dense, erect to semi-erect, 0.32–0.35 mm long hairs with numerous short branches, hairs obscuring surface on apical 4/5 of clypeus; hair of supraclypeal area very short (0.04–0.08 mm), sub-appressed, sparse; hairs of parocular area and lateral areas of frons similar to those of clypeus but sparser, not obscuring surface; mandibular fringe weak, hairs 0.22–0.35 mm long, sparse ; T1-4 with narrow apical fascia of appressed, short hairs; fascia broadly interrupted on T1, more narrowly on T2, complete on T3-4, although often worn medially; discs of T1-7 with very sparse, very short, erect hairs; S3–5 with apical fringe of posteriorly oriented fine hairs (very weak medially on S2); S3 with apicomedial triangular patch of appressed hair in area of medial emargination, triangular patch of very short, very fine hairs basal to this. *Color*: Black except claws, distal tarsomeres, and apex of mandible reddish brown; tibial

spurs translucent yellow; wings lightly infuscated, nerves brown.

Female: BL = 6.61 ± 0.54 mm , n = 43, 5.60–7.36; HW = 1.77 ± 0.10 mm, n = 75, 1.48–1.96. *Head*: Face approx. 1.07 × as broad as long, eyes convergent below (UIOD 1.3 × LIOD). Clypeus similar to male but punctures shallow, 0.5 to 1 PW apart. Punctation of supraclypeal area, parocular area, frons, vertex and gena similar to male but slightly less dense. Labrum similar to male but basal width 1.2 × length; apical width slightly less (0.9 ×) than length; basal 1/5 shiny, impunctate, distal 4/5 punctate. Lateral ocellus closer to vertex than to eye (OCED/OCVD = 1.4) with distance between lateral ocelli subequal to distance from lateral ocellus to eye. Scape slender, unmodified (scape length 3.5 × apical width); pedicel completely exposed; length flagellum (excluding pedicle) 2.5 × length scape; first five flagellar segments slightly shorter than broad, gradually increasing in length and width distally, segments 6–9 as long as wide, segment 10 1.8 × as long as broad. Gena as in male. Hypostomal area shiny, impunctate. Mandible tridentate, middle tooth slightly nearer lower tooth than upper. Mouthparts as in male. *Thorax*: As in male. *Abdomen*: Terga shiny, punctation and surface sculpture as in male. T1-6 with distal margins very narrowly impunctate. T6 nearly straight in lateral profile, with apical margin very narrowly produced, shelf-like. *Vestiture*: Hair entirely pale, similar to male on head and thorax except sparse, semierect on clypeus and parocular areas, not obscuring surface; hypostomal area fringed laterally by long, erect, apically recurved hairs. T1-4 with narrow apical fascia of appressed, short hairs; fascia broadly interrupted on T1, very weak medially on T2 and entire on T3 & 4 (although often worn away); T6 with dense semi-appressed simple hairs giving disc whitish appearance. Scopal hairs simple, erect. *Color*: As in male.

Material examined.—Holotype ♂: USA, **Texas**, Hidalgo Co., Bentsen-Rio Grande State Park, 29-iii-1991, J. L. Neff K09033 , deposited KSEM. Allotype ♀: same data except K09128, collecting mud, deposited KSEM. Paratypes: MEXICO: **Tamaulipas**: 6 ♂, Guemez, Hcda. Santa Engracia, 11-iii-1991, J. L. Neff, on *Prosopis glandulosa;* 1 ♂, same data except on *Salix nigra*; 2 ♂, same data except *on Persea americana*; Llera: 2 ♂, Ciudad Victoria, 16 mi. S, 18-iii-1987, J. L. Neff, on *Prosopis glandulosa* (all CTMI);. USA: **Missouri**: Jefferson Co.: 1 ♂, 1 ♀, La Barque Creek Core Area, T43NR3ES32 to (SE4), Sandstone Glades, 6-7-v-2006, M. A. Arduser, ex yellow pan trap; Shannon Co.: 3 ♂, 1 ♀, Ozark N. Riverway, Round Spring Area, T30NR4W sect 19, 10-v-1990, M. Arduser, on flowers of *Phacelia*; 1 ♂, Chitter Creek Preserve by Cook Hollow, T28NR1WS21, 4-v-1998, M. Arduser, on flowers of *Phacelia* (all MSAC); **North Carolina**: (Raines Co.): 5 ♂, Bryson City, 23-iv-1923, J. C. Crawford, on *Fragaria virginiana*; 1 ♂, same data except 1-v-1923 on *Potentilla canadense* (all AMNH); **Texas**: Austin Co.: 1 ♂, Stephen F. Austin S. P., 9-iv-1966, J. C. Shafter (TAMU); Bastrop Co.: 2 ♂, Sayersville, 15-iv-1987, J. L. Neff on *Nemophila sayersensis* (CTMI);; 1 ♀, same data but 2-iv-1995 on *Nemophila sayersensis* (CTMI); 1 ♀, Stengl Lost Pines Biological Station, 3-iv-2008, J. L. Neff, on *Rubus trivialis* (CTMI); Bee Co.: 3 ♂, 4 ♀, Pettus, 3-iv-1988, J. L. Neff, on *Phacelia congesta* (CTMI); Brazos Co.: 3 ♂, College Station, Lick Creek Park, 7-17-1987, J. Heraty & Woolley, ex intercept/Malaise (TAMU); 3 ♀, 17-30-iv-1987, Woolley & Heraty, ex intercept/Malaise (TAMU); Burleson Co.: 3 ♂, 4 ♀, Burleson, 3 mi. N, J. L. Neff (CTMI), 8-iv-1986, on *Nemophila sayersensis*; Dimmit Co.: 6 ♂, 1 ♀, Carrizo Springs, 6 mi. E, 31-iii-1994, J. L. Neff and A. Hook (CTMI); Goliad Co.: 2 ♂, Charco, 1 mi. W, 18-iv-1987, J. L. Neff (CTMI), on *Nemophila phacelioides*; 1 ♀, same data but on *Phacelia congesta* (CTMI); Grimes Co.: 4 ♂, 2 ♀, Navasota, 2 mi. N, 6-iv-1988, J. L. Neff, on *Nemophila phacelioides* (CTMI); Hidalgo Co.: 1 ♂, same data as holotype (USNM); 23 ♀, same data as allotype (CTMI); 1 ♀, same data (USNM); 4 ♂, same data except 17-iii-1989 on *Lepidium virgatum* (CTMI); 7 ♂, same data except 17-iii-1989 on *Teucrium cubanense* (CTMI); 15 ♂; 1 ♀, same data except 16-iii-2007 (CTMI), on *Salix nigra*; 1 ♂, same data except 16-iii-2007 on *Ehretia anacua*

(CTMI); 7 ♂, 6 ♀same data except 19-iii-1992, A. W. Hook and C. R. Nelson (BFLC), no host; 2 ♂, same data except 15-iii-1982, C. Porter (FSCA); 3 ♂, same data except 16-iii-1982 (FSCA); 1 ♂, 1 ♀, same data except 17-iii-1982 (FSCA); 6 ♂, 1 ♀, same data except 23-iii-1984 (FSCA); 3 ♂, same data except 22-iii-1985 (FSCA); Karnes Co.: 1 ♂, Panna Maria, 1 mi. S, 18-iv-1987, J. L. Neff, on *Nemophila phacelioides* (CTMI); Lee Co.: 2 ♂, Fedor, 7-iv-1919, Birkmann (KSEM); 2 ♂, 1 ♀, Lexington, 1 mi. N, 8-iv-2005, J. L. Neff, on *Nemophila sayersensis* (CTMI); Washington Co.: 1 ♂, Washington, 3 mi. W, 8-iv-1987, J. L. Neff, on *Nemophila phacelioides* (CTMI); 1 male, Pickens Rd., 2.75 mi. N of rt. 105, 12-iii-2000, Panero, Crozier and Helfgott, on *Nemophila phacelioides* (CTMI); Zapata Co.: 1 ♀, San Ygnacio, 30-iii-1991, J. L. Neff and A. Hook, on *Phyla strigulosa* (CTMI); 1 ♀, San Ygnacio, 13 km N, (Arroyo Dolores), 2-iv-1994, A. W. Hook (BFLC). Other specimens: MEXICO: **Tamaulipas**: (Padilla), 12 ♂, 14 ♀, Rio Corona, 18 mi. N. of Ciudad Victoria, 1977, R. Schmidt (BLCU); USA: **Arkansas**: (St. Francis Co.), 2 ♂, Forest City, 11-iv-1946, C. D. Michener (KSEM); **Indiana**: Posey Co.: 2 ♂, Hovey Lake, Ent Recons. Station 12, 13-v-1958 (PURC); **Texas**: Colorado Co., 1 ♂, Columbus, 2-iv-1947, H. Townes (KSEM); Gonzalez Co.: 2 ♂, Luling, 30-iii-1951, R. H. Beamer, on *Salix* (KSEM); 1 ♂, same data (NCSU); 1 ♂, 2 ♀, Palmetto State Park, 5-iv-1954, R. E. Beer & party (KSEM); Hidalgo Co.: 1 ♂, Bentsen-Rio Grande S. P., 14-iii-1983 (BLCU), C. Porter; 1 ♂, same data except 15-iii-1983 (BLCU); 2 ♂, 1 ♀, same data except 17-iii-1983 (BLCU).

Discussion.—This species is described to include the males associated with *Hoplitis simplex* by Mitchell (1962). The justification for this is given in the discussion of *Hoplitis simplex*. Although broadly sympatric with *Hoplitis simplex* in the south-central United States, *H. nemophilae* has a more southerly distribution than *H. simplex*, ranging from southern Indiana to central Tamaulipas (Fig. 1). The name *nemophilae* refers to *Nemophila* (Boraginaceae: Hydrophylloideae), the flowers this species is mostly commonly associated with in central Texas. Despite the name, the species is probably not oligolectic on *Nemophila*, or even more generally oligolectic on the Hydrophylloideae. None of the collections from the southernmost portion of its range (southern Texas and Mexico) have been from *Nemophila* or other Hydrophylloideae. In fact, no *Nemophila* or *Phacelia* species were flowering in the vicinity of my collections of *H. nemophilae* in south Texas and Tamaulipas. The few pollen records from this area suggest that *Prosopis* (Fabaceae) and *Rubus* (Rosaceae) are pollen hosts in the absence of Hydrophylloideae. Females were also observed at male catkins of *Salix nigra* Marsh. in south Texas, although none bore scopal pollen loads. Like other *Robertsonella*, *Hoplitis nemophilae* is a vernal species, active from mid March through mid April (in Texas) but as late as early June in the northern part of its range (Indiana).

Nests are unknown but numerous females of *Hoplitis nemophilae* were observed gathering mud at communal mud-gathering sites on the banks of resacas (oxbow lakes), wildlife watering areas and the Rio Grande at Bentsen-Rio Grande State Park, Hidalgo Co., Texas indicating that it, like *H. simplex*, uses mud for nest construction.

KEY

MALES

1. Clypeal pubescence of very short (0.08–0.10 mm), branched, dense, appressed hairs, hairs particularly dense on apical half; mandibular fringe of hairs on lower margin of mandibles long (max. length 0.53–0.65 mm) and dense (Fig. 2); S3 with a very shallow, median emargination, area of emargination with triangular patch of semi-appressed setae (Fig. 4); mandibles broad basally, basal width 0.4 × eye length .... *H. simplex* **(Cresson)**

Fig. 2. Head of *Hoplitis simplex* male, lateral view.
Fig. 3. Head of *Hoplitis nemophilae* male, lateral view.
Fig. 4. S3 of *Hoplitis nemophilae* male.
Fig. 5. S3 of *Hoplitis micheneri,* male.

1a. Clypeal pubescence longer (0.32–0.36 mm), erect to suberect; mandibular fringe short (max. length 0.22–0.35 mm) and thin (Fig. 3); S3 variable; base of mandible narrower, basal width narrower, 0.3 × eye length 2

2. Apical margin of S3 nearly straight, emargination very weak, area of emargination with triangular patch of semi-appressed white hair (Fig. 4) .... ***H. nemophilae*** **Neff**

2a. Apical margin of S3 deeply emarginate, emargination approximately ¼ as broad as sternum and lined with a dense fringe of long white hair (Fig. 5) .... ***H. micheneri*** **Mitchell**

FEMALES

1. Punctation of T1 very fine and sparse, punctures 4+ PW apart on disc; scutellum with narrow, impunctate antero-median depression .... ***H. micheneri*** **Mitchell**

2. Punctation of T1 fine and deep, punctures 2–3 PW apart on disc, scutellum uniformly punctate .... ***H. nemophilae*** **Neff** or ***H. simplex*** **(Cresson)***

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* Females of *nemophilae* and *simplex* cannot be reliably separated without associated males.

BIOLOGY OF *HOPLITIS SIMPLEX*

Nests and nest construction.—*Hoplitis simplex* is a cavity renting species. There is no evidence it ever excavates its own burrows in pithy stems like some other *Hoplitis* (Rau 1928; Michener 1955). Natural nests have been observed in small diameter beetle galleries in tree branches and stems. *Hoplitis simplex* females also readily accept trap nests bored in pine blocks. Trap nest diameters utilized by *H. simplex* ranged from 2.8 to 4.8 mm. Larger diameter nests were present but not utilized by *H. simplex*. The diameter most frequently occupied by *H. simplex* was 3.2 mm during my observations but the nest arrays were not appropriate for determining nest size preferences. Reuse of nests, either of old *H. simplex* nests, or those of various mud-using eumenine wasps, was common.

Nests plugs, partitions, and sometimes wall linings, are constructed only of fine soil, without any added pebbles or vegetable material. Females have repeatedly been observed collecting mud at communal mud gathering areas at the edge of streams, seeps or ponds (Fig. 7). Numerous females repeatedly visited communal sites on the edge of streams or seeps to gather fine-grained mud. Such areas take on a honeycombed appearance from the many small tunnels and pits excavated by the mud collecting bees. This mud is held beneath the mandibles as a pellet on the smooth, hairless surfaces of the hypostomal area, a corbicula-like area fringed laterally by long curved hairs. In the absence of appropriate mud sources, *H. simplex* may create its own mud by adding fluids, probably regurgitated nectar, to dry soil. A single female was observed doing so near Sayersville, Bastrop Co., Texas. Many of the soil-gathering trips (discussed below) timed at BFL seemed to be too brief to allow for flight to distant mud sites. Moreover, tests of the partitions proved positive for sucrose, although this could have been contamination from the provisions or added later while the bee was working in the nest.

Nest architecture varies with the relationship of bee body diameter and nest diameter. When bee body diameter and nest diameter are similar, nests are simple linear arrays of cells separated by soil closed with an outer mud plug. Occasionally, when the cross-sectional diameter of the bee is significantly smaller than the diameter of the cavity she is using (such as in 4.8 mm diameter trap nests), she may line the cell walls with mud to create cells whose diameter more closely matches her own. In 60% of the measured nests, the posterior end of the nest was indicated by a relatively thin (1.4 ± 1.3 mm, n = 7) soil partition. In borings less than 50 mm long, this was almost always flush with the end of the boring, but in longer holes this final partition often was placed some distance in front of the end of the boring. Vestibular cells (length = 15.0 ± 9.0 mm, 5.1–42.0, n = 18) were present in 58.3% of the nests. Eighty percent of the nests in 100 mm long borings had vestibular cells compared to only 50% of the nests in borings less than 50 mm long. In addition to the vestibular cells, short intercalary cells were observed in 5% (2 of 38) of the nests. The number of cells per nest averaged 7.9 ± 2.1 (n = 10, 5–11) in 100 mm long borings and 2.5 ± 1.0 (n = 26, 1–4) for borings less than 50 mm. Cell length averaged 9.0 ± 2.3 mm (n = 73, 5.2–19.7). No position-specific significant differences were found between lengths of cells within the nests. The cell partitions are concave on their anterior surface, flat posteriorly, rather thin medially (0.5 ± 0.1 mm, n = 8, 0.4–0.6) and wider on the cell walls (1.4 ± 0.7 mm, n = 7, 0.5–2.3). The cell plug was rather short (4.0 ± 1.5 mm, n =27, 1.2–7.5) and flush with the entrance in 39.4% of the nests. In the remaining nests it was slightly recessed (2.5 ± 1.4 mm, n = 9, 1.0–4.2) from the entrance.

Females averaged 2.70 ± 2.33 min per trip (0.03–24.35, n = 388) for soil collecting

trips and spent an average of 2.07 ± 2.68 min (0.03–25.00, n = 380) in the nest constructing cell partitions or nest plugs. Time spent gathering mud at communal sites averaged 21.8 ± 6.1 sec (12.7–37.5, n = 30). It took an average of 10.7 ± 5.0 soil gathering trips (5–24, n = 12) to construct a partition in a 3.2 mm diameter nest, 12.5 ± 2.9 (8–16, n = 6) for 4.0 mm nests and 10 trips (n = 2) for 4.8 mm nests. Usually only two trips were required to close a cell and the remaining trips were for adding additional soil to the partition or cell walls. Time to construct a partition in a 3.2 mm diameter nest averaged 52.27 ± 26.08 min (24.00–106.97, n = 12), 80.35 ± 27.38 min (57–117, n = 6) in 4.0 mm nests and 52.00 ± 11.31 min (44.00–60.00 min, n = 2) for 4.8 mm nests. Times and number of trips for constructing partitions in the 4.8 mm nests are not strictly comparable to those for the 3.2 and 4.0 mm nests because the former had previously been occupied by eumenine wasps and had pre-existing partial partitions, while the latter nests were previously unoccupied. Nest closure (sometimes the closure for the last cell plus the cell plug when a vestibular cell was present) required an average 22.67 ± 5.61 trips (14–34, n = 9) for 3.2 mm nests, 22 trips (n = 1) for 4.0 mm nests and 34 trips (n = 1) for 4.8 mm nests. Time to complete the closure averaged 83.07 ± 25.59 min (43.9–148.77, n = 9) for 3.2 mm nests, 123.67 min (n = 1) for 4.0 mm nests and 127.1 min (n = 1) for 4.8 mm nests. The basal partition of a 3.2 mm nest was accurately timed only once and required 2 trips and 14 min.

Intrafloral behavior.—Visits to flowers of *Nemophila phacelioides*, the primary host of *Hoplitis simplex* at BFL, are typically brief. Females foraging at midday on flowers of *N. phacelioides* at BFL averaged 5.5 ± 4.1 sec (n = 50, 0.9–19.6) for nectar and pollen collecting visits and 4.8 ± 2.9 sec (n = 15, 0.9 = 9.4) for nectar only visits. The pale blue flowers of *N. phacelioides* have rotate corollas with five erect stamens and five nectaries. The nectaries are located between the anther bases and are hidden by scales. Females of *H. simplex* are able to simultaneously forage for pollen and nectar by perching on individual anthers (Fig. 8). A female scrapes pollen directly from the anthers into her abdominal scopa using her hind legs while tapping the anthers with her abdomen. At the same time, she inserts her mouthparts into the nectary below. Unlike females of *Andrena sagittagalea* Ribble, another bee common on *Nemophila* in central Texas, *H. simplex* females do not vibrate or buzz the anthers of *N. phacelioides* while harvesting pollen.

Hoplitis simplex is not an early foraging bee, at least at BFL. Foraging by females usually begins after 1000 AM, a time that corresponds with the usual initiation of nectar production in *N. phacelioides* flowers at BFL. Pollen availability from *N. phacelioides* continues through the day as anther dehiscence and floral anthesis occurs asynchronously; foraging continues until near dusk.

Provisioning.—Females of *Hoplitis simplex* are able to construct and provision up to three cells per day, although typically they complete only one or two. On average it took 10.8 ± 1.8 (7–15, n = 27) pollen trips to provision a cell. The distribution of pollen trips per cell was unimodal (mode of 10) with 85.2% of the provisioning series entailing 9–12 pollen trips. The mean duration of a pollen collecting trip was 8.38 ± 4.59 min (1.50–33.02, n = 320). For individual cell provisioning series, the mean duration of a pollen collecting trip ranged from 3.21 to 17.50 min with mean trip duration decreasing through the day (Mean Trip Duration = 28.222–1.506 × Start Time, r^2 =0.468, F = 0.0003). Time to provision a cell (including time in the nest) averaged 114.11 ± 40.02 min (61.00–192.60, n = 27). Although the correlation is weaker, provisioning time per cell also decreased through the day (Provisioning Duration per Cell = 280.05–12.402 × Start Time, r^2 = .262, F = 0 .0063

Females averaged 2.49 ± 3.48 min (0.14–46.78, n = 313) in the nest between provisioning trips. As in many other megachilid bees, females typically would deposit nectar into the provision mass, working it with her mandibles, then, if the nest was too narrow to permit turning around within the nest, back out of the nest, turn around and back in to deposit pollen. The initial nectar deposition phase averaged 0.85 ± 0. 41 min (0.08–3.50, n = 285) and pollen deposition averaged 1.54 ± 3.03 min (0.17–46.28, n = 254). After the last pollen trip of a provisioning series, the female usually made a short final trip, presumably for nectar, averaging 1.90 ± 2.14 min (0.08–9.28, n = 26). Upon returning from this last trip, she spent 1.35 ± 0.96 min (0.48–5.47, n = 26) in the nest depositing nectar. She then turned around, backed in and spent 1.14 ± 0.60 min (0.38–3.15, n = 29) in the nest, during which time oviposition occurred.

Development and cocoon construction.— The slightly wider posterior end (0.6 mm vs. 0 5 mm anteriorly) of the slightly curved, 2 mm long egg is inserted into the slanting upper face of the provisions (Fig. 6). Eclosion occurs 3–4 days after oviposition. The first evident instar (presumably the second larval instar since in most LT bees the first molt occurs within the chorion (Torchio 1989, Trostle and Torchio 1994)) bends downwards and begins feeding within a few hours of eclosion. This instar has a HW of 0.40 mm. If we start the development clock as day 0 at eclosion, the molt to the third larval instar (with a HW of 0.48 mm) occurs on day 2, the molt to the fourth larval instar (HW = 0.60 mm) occurs on day 4 and the final larval molt to the fifth instar (HW = 0.70 mm) on day 6 or 7. Throughout this initial period, the glabrous larva feeds while remaining attached to the provision mass at the original place of insertion of the egg, gradually excavating an antero-ventral cavity in the provision mass. The fifth larval instar, easily recognizable by its setose integument, initially remains attached to the place of egg insertion, continues feeding, and begins defecating the day after the fourth molt (day 7 or 8). Fecal pellets are pale yellow, smooth, slightly arched, truncate cylinders averaging 0.44 ± 0.11 mm long (0.70–0.10, n = 30) and 0.22 ± 0.02 mm in diameter (0.24–0.18, n = 30). It continues feeding and defecating while attached to the provision mass for another three or four days (days 10–12) before releasing itself and beginning to move over the remaining provision mass. The larva continues moving, feeding and defecating for another three to four days. On day 13–16, in addition to the previously mentioned activities, the larva begins to construct the operimentum (Mathews 1965), a translucent, secreted lining adhering closely to the anterior partition and adjacent walls of the cell (Fig. 9). Intermittent feeding and operimentum construction continues for another 10 days or so (to days 23–26) until a strong lining has built up on the anterior portion of the cell walls, and the provisions are consumed (or nearly so). The larva then begins cocoon construction by spinning a delicate collar or hood-like structure attached to the edges of the anterior cell partition and slanting posteriorly to what will become the anterior portion of the cocoon (Fig. 9). Since the collar occupies the space between the anterior end of the cocoon and the anterior cell partition, its length varies with cell and cocoon size. In relatively short cells (7 mm or less) it may be little more than a rim of silk connecting the cocoon to the operimentum. Usually, most of the feces are loosely contained between the sides of collar and the cell walls, although in some, nearly all is trapped between the sides of cocoon and the cell walls. Upon completing this structure, the larva begins working on the cocoon walls, creating a tough, single layered, translucent, cylindrical structure with a rounded anterior end. The cocoon usually contacts the cell walls laterally and

Fig. 6. *Hoplitis simplex* provision mass with egg.
Fig. 7. *Hoplitis simplex* females at mud collection site.
Fig. 8. *Hoplitis simplex* female foraging for nectar and pollen on flower of *Nemophila phacelioides*.
Fig. 9. Cocoon of *Hoplitis simplex*: a - operimentum; b - collar (torn); c - cocoon proper; d - fecal pellets; e - cell partition.

lacks an obvious nipple or anterior thickening. The precise shape of the cocoon depends on whether or not its posterior end contacts the posterior cell partition, conforming to shape of the partition if it does, and more oval if it does not. Cocoon construction requires five to six days. Upon completing the cocoon, the larva enters a dormant state, in which it remains until the following spring, when it pupates and emerges from the nest.

Emergence and sex ratio.—*Hoplitis simplex* is clearly protandrous. 1988 emergence from a set of nests maintained under ambient conditions and provisioned in 1987 occurred over 7 days (1–7 April) with 81.6% (31 of 38) of the males emerging in the first 3 days before the first female emerged. The overall sex ratio was 2.92 M: F. In 1989, bees from nests provisioned in 1988 emerged over a 15 day period, interrupted by a 6 day cold spell when daily highs did not exceed 15° C and no emergence occurred. Again, 91.2% (52 of 57) males emerged in the first four days of emergence, while only 7.1% (3 of 42) females did so during the same period. The 1989 sex ratio was 1. 35 M: F and the combined 1988+1989 sex ratio was 1.72. An average male of *H. simplex* from BFL was lighter (dry weight = 4.4 ± 0.7 mg, n = 7, 3.6–5.4) than the average female (6.5 ± 1.1 mg, n = 23, 3.2–8.4), even though the smallest female was lighter than the smallest male. If, as is commonly assumed, investment is proportional to dry mass, then the expected M:F sex ratio based on adult dry weights would be 1.48:1. This is close to the observed 1989 ratio but quite different from that in 1988. The available

data are inadequate to resolve this discrepancy.

Males and mating.—Male *Hoplitis simplex* patrol and forage at flowers utilized by the females. They were not observed patrolling nest sites, emergence sites or mud collecting areas. The few observations of mating suggest it is very perfunctory. A patrolling male would pounce on a female when she landed on a flower. This was followed by a brief period of copulation with the male leaving without any mate guarding or post-copulatory mating display.

Parasites and predators.—Females of a small, undescribed *Stelis* sp. (F. Parker, pers. com.) were repeatedly observed at the entrances of *Hoplitis simplex* nests at BFL and occasionally entering the nests. In one dissected nest, the *Stelis* egg was placed at the rear of the cell and the hairy, motile last larval instar was the hospicidal form that killed the host. Several males and females of the undescribed *Stelis* were reared from *H. simplex* nests and others were detected in nest dissections by their distinctive nippled cocoons and dark fecal pellets. The report of *Stelis lateralis* being reared from a *Hoplitis simplex* nest from Nebraska (Hurd 1979, Swenk 1914) is almost certainly based on a misidentified *Alcidamea* nest as I know of no valid records for *Robertsonella* from this area.

The outermost cells of some completed nests of *Hoplitis simplex* at BFL were occasionally destroyed by raiding fire ants (*Solenopsis invicta* Buren), although they rarely destroyed the inner cells.

DISCUSSION

The nesting biology of the Osmiini is famously diverse with some species excavating nests in the soil, others excavating nests in pithy stems, many using pre-existing cavities and some constructing free standing mortar nests (Michener 2007). Materials used in nest construction include various combinations of resin, pebbles, soil, masticated leaves, petals and wood chips (Michener 2007). Cavity nesting appears to be plesiomorphic in the Osmiini as it is widespread, perhaps universal, in the basal *Chelostoma* and heriadine lineages (Michener 2007; Praz et al. 2008), but it may be secondarily derived in *Hoplitis* where nests excavated in soil are common in several basal lineages (Praz et al. 2008). The nests of *Hoplitis simplex* (and probably other *Robertsonella*), constructed in pre-existing cavities with mud, without any pebbles or plant material or other amendments, appear to be unique in *Hoplitis* (the vast majority of whose reported nests are constructed with masticated plant parts, often with additional materials) and unusual in the Osmiini (Michener 2007), found elsewhere only in *Chelostoma* (Parker 1988) and some *Osmia* species (Bosch et al. 2001; Cane et al. 2007). The use of soil for nest construction by *Robertsonella* appears to be derived within *Hoplitis* but this will require more data on the nests of other *Hoplitis* taxa and a better understanding of the phylogenetic position of *Robertsonella*. Our understanding of the phylogeny of *Hoplitis* has recently been greatly enhanced by a molecular analysis of the Osmiini (Praz et al. 2008) which included representatives of 18 of the 27 subgenera of *Hoplitis* recognized by Michener (2007). Unfortunately, *Robertsonella* was not one of the included subgenera.

The distinctive cocoons of *Hoplitis simplex*, with the operimentum, collar and nipple-less, single layered, inner cocoon appear to be quite similar to those reported for *H. (Cyrtosmia) hypocrita* (Cockerell), *H. (Monumetha) fulgida* (Cresson) and *H. (Alcidamea) sambuci* Titus (Clement and Rust 1976). The inner cocoons of *H. hypocrita* and *H. fulgida* differ from those of *H. simplex* in having nipples, and all three differ in that the collar connecting the operimentum (the collar of Clement and Rust 1976) to the inner cocoon is a network of threads, rather than the mixture of threads and sheet-like material in the collar of *H. simplex*. The cocoons of members of *Acrosmia* (Parker 1978), *Dasyosmia* (Rust 1980), *Formicapis*

(Rust and Clement 1975), *Hoplitis s. str.* (Eickwort 1973), and the *Proteriades* group (*Hoplitina*, *Penteriades* and *Proteriades*) (Parker 1978) all lack an operimentum or a collar. The outer cocoons of this latter group of taxa may be homologous with the operimentum, but at least in *H. (Hoplitis) anthocopoides* (Schenck), it is spun after the completion of feeding (Eickwort 1973), rather than shortly after the fifth molt as in *H. simplex*. Using the molecular analysis of Praz et al. (2008) as a framework, cocoon structure suggests that *Robertsonella* will be found to be more closely related to the clade including *Alcidamea*, *Cyrtosmia* and *Monumetha*, than the larger, mainly old world clade including *Formicapis* and the *Proteriades* group.

There are very few data available on the foraging behavior of other *Hoplitis* species. A notable exception is the report of Strickler (1979) on *H. (Hoplitis) anthocopoides* (Schenck), a specialist on *Echium* (Boraginaceae). She found that *H. anthocopoides* collected about the same amount of pollen per visit as individuals of several similarly sized generalist bee species, but it spent much less time per flower and less time moving between flowers and stalks of its preferred host than did the generalists. She noted that the increased foraging speed might require increased energy expenditure, and hence increased time spent foraging for nectar. However, in the case of *H. anthocopoides*, increased time costs would be minimal since it harvests nectar and pollen simultaneously. This advantage probably also applies to *H. simplex* since it also simultaneously harvests pollen and nectar.

In *Robertsonella*, *Hoplitis micheneri* appears to be is an oligolege of *Amorpha*, *H. simplex* appears to be oligolectic on the Hydrophylloideae and *H. nemophilae* is polylectic with a strong preference for the Hydrophylloideae. The status of *H. simplex* as oligolectic is tentative since there are very few floral records from the northern part of its range. With more data, it may prove to be like polylectic like *H. nemophilae*, again with a strong preference for the Hydrophylloideae. Interestingly, no *H. micheneri* have been reported visiting any Hydrophylloideae while no *H. simplex* or *H. nemophilae* have been reported visiting *Amorpha*, although both plant groups are widespread and occur in the ranges of all three bee species. Phylogenetically distant, the flowers of both groups do share the characters of short, exserted anthers. Females of *H. simplex* and *H. nemophilae* are able to perch on *Nemophila* and *Phacelia* anthers and simultaneously collect pollen and nectar. Foraging behavior of *H. micheneri* has not been reported but I expect similar behavior on the flowers of *Amorpha*, which are superficially similar to *Phacelia* flowers. Flowers of *Prosopis* and *Salix*, suspected floral hosts of *H. nemophilae*, share the same morphology.

At 10.8 trips per cell, *Hoplitis simplex* falls very close to the mean number of trips per female cell for all bees ($x = 11.66 \pm 8.84$, $n = 72$, 2–40, median = 9.25, data set of Neff (2008)). However, it is more than the mean number of trips per cell for other small (body dry weight < 10 mg) bees ($x = 6.13 \pm 3.40$, $n = 27$, 2–17, median = 5.0). Although the data set is too small for firm conclusions, megachilids have a higher mean number of trips per cell ($x = 23.24 \pm 10.66$, $n = 15$, 10–40, median = 17.60) versus that of all other bees ($x = 8.76 \pm 5.11$, $n = 57$, 2–22, median = 8.00). This high number of trips suggests that either megachilids require more pollen per cell than other bees, or more likely, their ventral scopae have a smaller pollen transport capacity than bees with other means of external pollen transport.

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LITERATURE CITED

Bosch, J., Y. Maeta, and R. Rust. 2001. A phylogenetic analysis of nesting behavior in the genus *Osmia* (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* 94: 617–27.

Cane, J. H., T. Griswold, and F. D. Parker. 2007. Substrates and materials used for nesting by North American Osmia bees (Hymenoptera: Apiformes: Megachilidae). *Annals of the Entomological Society of America* 100: 350–58.

Clement, S. L. and R. W. Rust. 1975. The biology of *Hoplitis robusta* (Hymenoptera: Megachilidae). *Entomological News* 86: 115–20.

———. 1976. The nesting biology of three species of *Hoplitis* Klug. *Pan-Pacific Entomologist* 52: 110–19.

Cockerell, T. D. A. 1909. Descriptions and records of bees. -XXI. *Annals and Magazine of Natural History, ser. 8* 4: 25–31.

Cresson, E. T. 1864. On the North American species of several genera of Apidae. *Proceedings of the Entomological Society of Philadelphia* 2: 373–411.

Eickwort, G. C. 1973. Biology of the European mason bee, *Hoplitis anthocopoides* (Hymenoptera: Megachilidae) in New York state. *Search: Agriculture* 3: 1–32.

Graenicher, S. 1909. Wisconsin Flowers and their pollination: Compositae, Part I. *Bulletin of the Wisconsin Natural History Society* 7: 19–77.

Griswold, T. L. and C. D. Michener. 1998. The classification of the Osmiini of the Eastern Hemisphere (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society* 70: 207–53.

Gupta, R. K. 1991. On genus *Robertsonella* Titus, with a description of a new species from Himachal Pradesh, India (Insecta, Hymenoptera, Apoidea - Megachilidae). *Reichenbachia* 28: 173–75.

———. 1999. *Taxonomic Studies on the Megachilidae of North-Western India*. Scientific Publishers (India), Jodhpur. 291 pp.

Hurd, P. D. Jr., W. E. LaBerge, and E. G. Linsley. 1980. Principal sunflower bees of North America with emphasis on the southwestern United States (Hymenoptera: Apoidea). *Smithsonian Contributions to Zoology* 310: 158 pp.

———. 1979. Superfamily Apoidea. Pp. 1741–2209 *in* Krombein, K. V., P. D. Hurd, Jr, D. R. Smith, and B. D. Burks, eds. *Catalog of Hymenoptera in America North of Mexico*. Smithsonian Institution Press, Washington, D. C.

——— and C. D. Michener. 1955. The megachiline bees of California (Hymenoptera: Megachilidae). *Bulletin of the California Insect Survey* 3: 1–247.

Matthews, R. W. 1965. The biology of *Heriades carinata* Cresson (Hymenoptera, Megachilidae). *Contributions of the American Entomological Institute* 1: 1–33.

Michener, C. D. 1938. The bees of the genera *Chelostomopsis, Formicapis, Robertsonella,* and *Prochelostoma* (Hymen.: Megachilidae). *Entomological News* 49: 127–32.

———. 1941. A generic revision of the American Osmiinae with descriptive notes on Old World genera (Hymenoptera: Megachilidae). *American Midland Naturalist* 26: 147–76.

———. 1947. A revision of the American species of *Hoplitis* (Hymenoptera, Megachilidae). *Bulletin of the American Museum of Natural History* 89: 257–318.

———. 1955. Some biological observations on *Hoplitis pilosifrons* and *Stelis lateralis* (Hymenoptera, Megachilidae). *Journal of the Kansas Entomological Society* 28: 81–87.

———. 2007. *The Bees of the World*. The Johns Hopkins University Press, Baltimore. xvi + 953 pp.

Mitchell, T. B. 1962. Bees of the Eastern United States, Volume II. *North Carolina Agricultural Station Technical Bulletin* 152: 1–557.

Neff, J. L. 2004. Hooked hairs and not so narrow tubes: two new species of *Colletes* Latreille from Texas (Hymenoptera: Apoidea: Colletidae). *Journal of Hymenoptera Research* 13: 250–261.

———. 2008. Components of nest provisioning behavior in solitary bees (Hymenoptera: Apoidea). *Apidologie* 39: 30–45.

Parker, F. D. 1978. Biology of the bee genus *Proteriades* Titus (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 51: 145–73.

———. 1988. Nesting biology of two North American species of *Chelostoma* (Hymenoptera: Megachilidae). *Pan-Pacific Entomologist* 64: 1–8.

Pearson, J. F. W. 1933. Studies on the ecological relations of bees in the Chicago region. *Ecological Monographs* 3: 373–441.

Praz, C. J., A. Müller, B. N. Danforth, T. L. Griswold, A. Widmer, and S. Dorn. 2008. Phylogeny and biogeography of bees of the tribe Osmiini (Hymenoptera: Megachilidae). *Molecular Phylogenetics and Evolution* 49: 185–97.

Rau, P. 1928. The nesting habits of the pulp-making bee, *Alcidamea producta* Cress. *Psyche* 100–07.

Rust, R. W. 1980. Nesting biology of *Hoplitis biscutellae* (Cockerell) (Hymenoptera: Megachilidae). *Entomological News* 91: 105–09.

Strickler, K. S. 1979. Specialization and foraging efficiency of solitary bees. *Ecology* 60: 998–1009.

Swenk, M. H. 1914. I. Studies of the North American bees. II. Family Stelididae. *Nebraska University Studies* 14: 1–36.

Titus, E. S. G. 1904. Notes on Osmiinae with description of new genera and species. *Journal of the New York Entomological Society* 12: 22–27.

Torchio, P. F. 1989. In-nest biologies and development of immature stages of three *Osmia* species (Hymenoptera: Megachilidae). *Annals of the Entomological Society of America* 82: 599–615.

Trostle, G. and P. F. Torchio. 1994. Comparative nesting behavior and immature development of *Megachile rotundata* (Fabricius) and *Megachile apicalis* Spinola (Hymenoptera: Megachilidae). *Journal of the Kansas Entomological Society* 67: 53–72.